

Biology and Life Cycle of *Siganus vermiculatus* (Siganidae, Pisces)¹

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ABSTRACT: The herbivorous fish *Siganus vermiculatus* (Valenciennes) (Siganidae; Pisces), a mangrove swamp dweller, was studied in the field and in captivity in Fiji. The fish has a lunar spawning cycle, benthic sticky eggs, and pelagic larvae. Metamorphosis occurs between 23 and 27 days after hatching. The fry live in small schools in brackish or fresh water among mangrove roots. The young and adults are found mainly in shallow, murky water of mangrove swamps where they move in and out with the tides. The adults are sometimes seen in clear water near coral reefs or over sandy bottoms. Feeding takes place during the day and at night and consists mainly of grazing on algae and mangrove roots. A tolerance of extreme fluctuations in physicochemical parameters (temperature 19 to 38°C; salinity 2 to 55 ppt; dissolved oxygen 1.2 ppm; pH 6.2 to 8.4) permits the species to live in mangrove swamps.

THE RABBITFISH FAMILY SIGANIDAE consists of 27 known species (Woodland, pers. comm., 1979) of primarily herbivorous fishes (Lam 1974). Siganids occupy a wide range of habitats in the coastal waters of the tropical and subtropical Indian and western Pacific oceans.

Several studies on the biology and life cycle of siganids have been published since the fishes attracted worldwide attention as possible candidates for mariculture (Siganid Mariculture Group 1972, Lam 1974). Prominent publications include those of George (1972) on *Siganus rivulatus* (Forsk.) and *S. luridus* (Ruppell) in the Mediterranean, Popper and Gundermann (1975) on the same species and *S. argenteus* (Quoy and Gaimard) from both the Mediterranean and the Red Sea, and Hasse, Madraisau, and McVey (1977) on *Siganus canaliculatus* (Park) from Palau. No information is available on the biology of *S. vermiculatus* (Valenciennes) apart from two reports of experiments on its propagation in captivity (Popper, May, and Lichatowich 1976; Popper and Gundermann 1976).

The present study summarizes observations on the biology and life cycle of this species.

METHODS

The study was carried out between July 1973 and December 1975 as part of an effort to develop the culture of rabbitfish (Popper 1977), mainly in and near Raviravi on the northwestern coast of Viti Levu, Fiji (Figure 1). Some observations were also made near Suva and Ngau in Fiji (Figure 1), and in other western Pacific islands.

The study consists of (1) observations of adult and juvenile fish in the field and in captivity, (2) collection and sampling of adult fish for examination of gonadal state and stomach contents and of juveniles for records of size and growth, and (3) experiments in which larvae were reared.

The observations in the field were made in mangrove swamps, lagoons, and on coral reefs. They were carried out mainly at depths of up to 6 m, as the fish were rarely seen in deeper water. In 1974 the observations were made at least once every 2 wk three times daily for periods of 45 to 60 min. Night observations in shallow water mangrove swamps were carried out by torchlight during receding and incoming tides.

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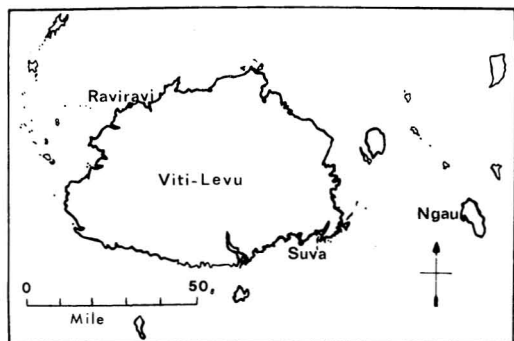


FIGURE 1. Partial map of the Fiji Islands. Sites of collections and observations.

Captive fish were held at Raviravi over periods of 3 to 12 mo for observation and breeding experiments (Popper 1977). The fish were reared in earthenware ponds (Popper 1977), cement tanks, and glass aquaria of 500 liters. Seawater was pumped into the tanks from a nearby tidal creek.

The fish maintained in the tanks and aquaria were fed in the morning and afternoon with a variety of foods, including commercial fish diets, algae (mainly *Sargassum* sp.), mosquito larvae, fly maggots, and rice bran. (In captivity the fish adapted easily to a wide range of diets.) No supplementary food was provided in the ponds, which were fertilized with organic fertilizers prior to filling with water (Popper 1977). Temperature, salinity, and pH level in the ponds and tanks were recorded twice daily. Fish in tanks and aquaria were observed at feeding time and whenever unusual activity or behavior was noticed.

Most fry were collected with hand nets around attractors, which consisted of bunches of grass hung under bamboo floats (Figure 2). Other methods used to collect fry and juveniles included hand netting while night torching in the mangrove swamps mainly on incoming tides; netting at high tide on the mud flats in front of the mangrove swamps and occasionally near coral reefs; spearing at night; and trapping the fish in shallow water by setting nets at night during high tide parallel and in front of the mangrove swamps.

Adult fish of various sizes were collected using the same methods used for fry or with

the help of commercial fishermen who used gill nets on the reefs.

Adult fish (10–30) were examined monthly. These fish were measured (standard length to 0.1 cm) and weighed (to 0.1 g for fry and 1.0 g for adults). Gonads were weighed and examined microscopically to define oocyte stages. Stomach contents were identified microscopically.

Methods used to induce spawning and to rear larvae are described elsewhere (Popper, May, and Lichatowich 1976; Popper and Gundermann 1976). Biopsies were conducted after spawning to determine which females had spawned.

RESULTS

Description

Siganus vermiculatus is one of the largest of the rabbitfishes: females can reach 45 cm and weigh 2.3 kg. The body of juveniles and adults is compressed and deep, the length 2.4 to 2.6 times the greatest body depth. This ratio declines with age and size. The length–weight relationship is defined by $W = 0.019 L^{3.1}$ (W , weight in g; L , total length in cm) (Figure 3). A dorsal fin with 13 spines and 10 soft rays and an anal fin with 7 spines and 9 rays are among the characteristic features of the family. A forward-directed spine is located in front of the dorsal fin. The caudal fin is emarginate. The small mouth is equipped with tiny incisor-like teeth. The body is covered with small embedded scales.

Coloration consists of a vermiculated pattern of brown lines on a silvery bluish background over the entire head and body, with a yellowish background on the head. This pattern becomes more complex and intricate with size and age (Figure 4, 1–5). Changes in color pattern occur during spawning and are described in the section on spawning behavior.

Geographical Distribution

Siganus vermiculatus is found in the tropical Indian and Pacific oceans. It has been recorded in the coastal waters of Fiji by Fowler



FIGURE 2. Preparation of grass bundles used to attract fry.

(1959). Woodland (pers. comm.) records it in north Australia and Palau, although it was not observed in Palau during the course of the present study. Herre and Montalban (1928) recorded it from the Philippines. Randall (pers. comm.) photographed a specimen in a market in Suluwesi, Celebes (Figure 5). It has not been observed or reported from the New Hebrides, New Caledonia, or the Solomon Islands despite similar climatic and ecological conditions. In these territories habitat similar to that used by *Siganus vermiculatus* is occupied by *S. lineatus* (Valenciennes), which is similar in size, habits, and some external features.

Biology and Life Cycle

The life cycle is here divided into arbitrary stages although in reality growth, development, and transitions are gradual (e.g., Figure 4, 1–5).

The eggs and larvae of *Siganus vermiculatus* are similar to those described and illustrated for other siganids, for example, *S. fuscescens* (Houttuyn) (Fujita and Ueno 1954), *S. oramin*

(Bloch and Schneider) (Soh and Lam 1973), *S. rivulatus* (Forsk.) (Popper, Gordin, and Kissil 1973), and *S. canaliculatus* (Park) (May, Popper, and McVey 1974) (Figure 6, 1–5).

The main difference noted between the larvae of *Siganus vermiculatus* and those of the other siganids was that 2 or 3 days before the end of the larval stages the larvae of *S. vermiculatus* began to resemble those of the postlarvae. These morphological features include a deeper body and longer spines in relation to body length (Figure 7) than are found in the larvae of the other species.

Duration of larval development in *Siganus vermiculatus* from hatching to metamorphosis is 23 to 25 days compared with 30 days or more for other siganids (Figure 8). Metamorphosis of larvae into fry occurs when the larvae are 18 to 26 mm long. The process of metamorphosis includes changes in coloration, behavior, and feeding habits. The transparent larvae, with only a few spots of black pigmentation (Figure 7), become fully pigmented postlarvae (Figure 4, 1) within 3 to 6 hr. The new pigmentation is arranged in

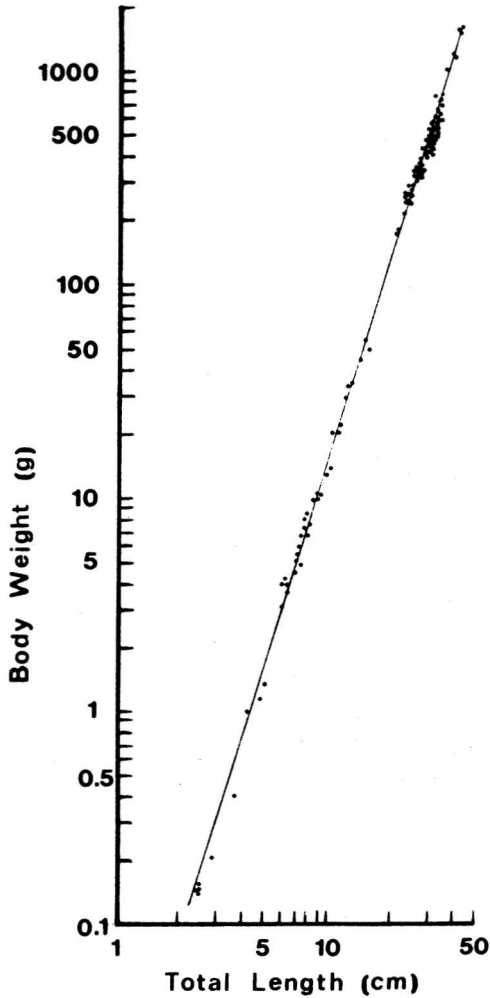


FIGURE 3. Length-weight relationship of *Siganus vermiculatus* ($N = 107$, $r = 95.8$, $W = 0.019 L^{3.1}$).

a simple form of the vermiculated pattern typical of *S. vermiculatus* (Figure 4, 1–5).

During and after metamorphosis the postlarvae gradually move from oceanic to coastal waters. Postlarvae were seined in ocean water together with a variety of species, including other siganids. Four such catches were made in the open sea, 2 to 15 mi offshore within the Fiji Islands, using light at night to attract fish for use as live bait. These larvae were caught the night before, or the night of, the new moon.

Postlarvae or early fry were collected daily off and around attractors (Figure 2) located

in front of the mangrove swamp at Raviravi. Most fry were collected during the 1st day of the new moon (Table 1). These observations indicate a lunar cycle in the shoreward migration of postlarvae, a cycle which coincides with the lunar spawning cycle described later and with the duration of larval development. The attractors were anchored 50 to 70 m offshore in front and between outlets of freshwater creeks (Figure 9). Most of the fry (83 percent) were collected off attractors stationed in front of the creeks where recorded salinities on the days of collection were slightly lower (12 to 15 ppt versus 13 to 21 ppt). The migration may thus be oriented toward brackish or freshwater creeks by a salinity gradient or currents of lower salinity. Newly metamorphosed fry were observed stationary between mangrove roots in such creeks a day or more after the first monthly appearance of fry at the attractors.

The attractors, the location of which was designed to intercept the assumed migration routes, served both as shelters and sources of food, as do mangrove roots when the fry reach them. Stomach contents of postlarvae collected around the attractors contained planktonic organisms (which constitute the diet of the oceanic forms) and epiphytic algae which grew on the attractors. Attractors with "seasoned" bundles of grass and abundant algal growth usually attracted more fry (78 percent) than newly installed ones. The stomach contents of fry collected between mangrove roots contained epiphytic algae and particles of root bark.

Larvae reared in captivity were observed to change their behavior during metamorphosis. Whereas the transparent captive larvae swam freely near the water surface or in the water column, pigmented postlarvae were seen stationary near and under floating leaves and other objects, or in the shade of the wall of the tank. At night they also were observed stationary near the same objects. Stomach contents of reared larvae included rotifers, copepods, and mosquito larvae. The stomach contents of postlarvae also contained filamentous algae and remnants of food flakes.

Both catches and observations suggest that the fry swim solitarily or in small groups.

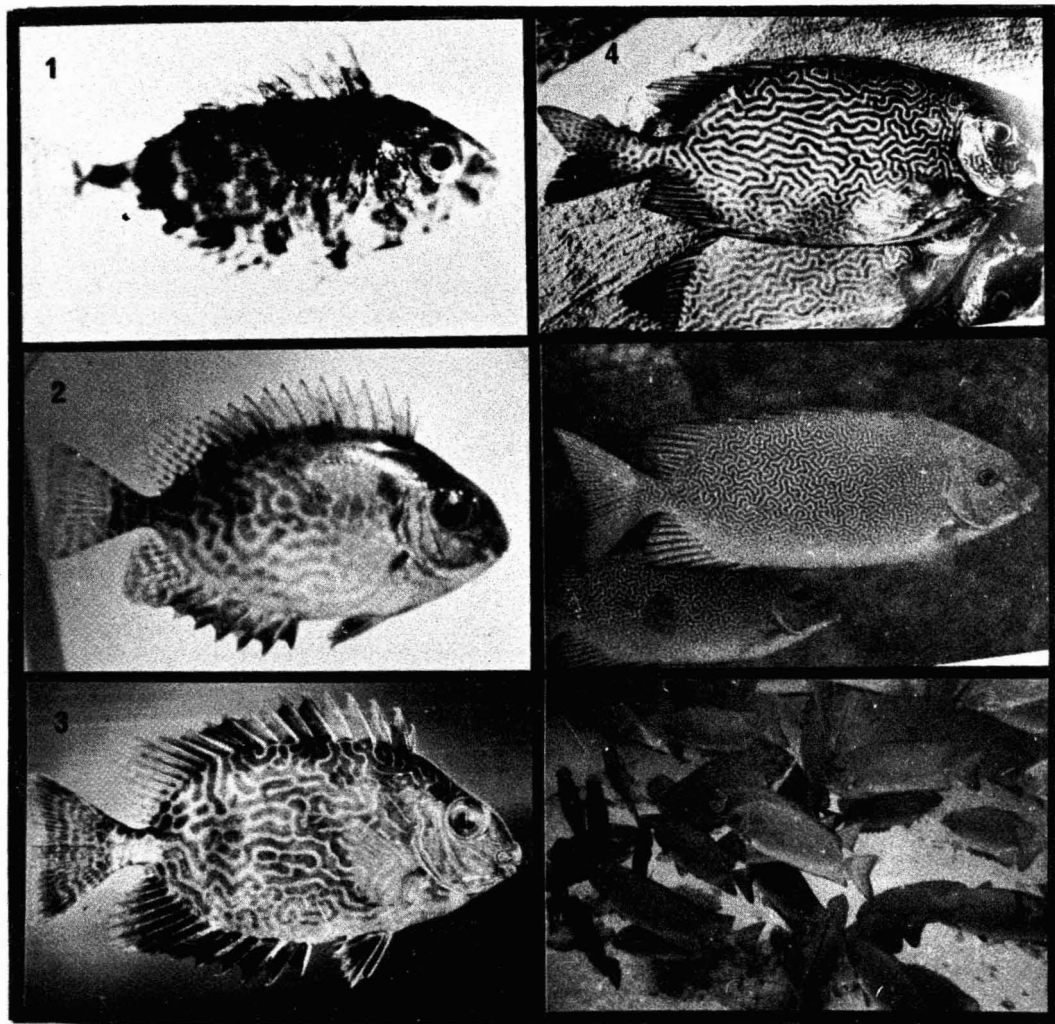


FIGURE 4. Development of vermiculated pattern in *Siganus vermiculatus*: (1) newly metamorphosed fry of 23 mm; (2) 2-mo-old juvenile of 53 mm; (3) 5-mo-old fish of 150 mm; (4) an adult fish of 23 cm; (5) an adult female of 40 cm (photographed in nature); (6) a school of adults of 35–40 cm during prespawning behavior (Ngau Island, Fiji).

There was no evidence that large schools were formed at this stage in the life history.

Observations and catches of fish smaller than 120 mm in length indicated that at this size *Siganus vermiculatus* is strictly a mangrove swamp dweller. Fry 25 to 30 mm in length were always seen among mangrove roots in creeks or other relatively deep spots which were not exposed at low tide. Fish of this size were observed and collected in nearly fresh water (2 ppt) in a creek near Suva

and frequently in brackish water in Raviravi. During the four following months, until they reached a length of 120 to 130 mm, the fish were seen mainly within the intertidal region, moving back and forth with the tide. These fish were collected mainly at night, during incoming and outgoing tides, in or near mangroves. The fish were seen singly or in small groups of up to four individuals. Fish less than 120 mm in length were never seen on reefs or in other habitats. The fish grazed on

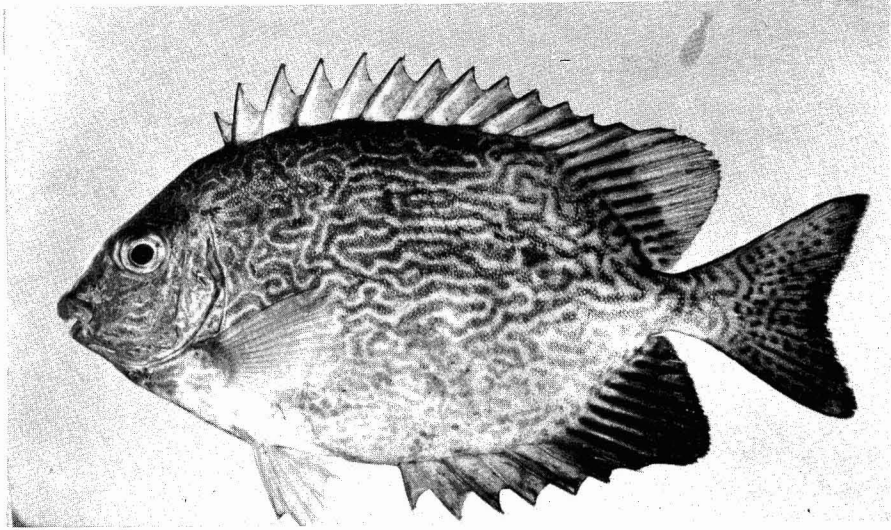


FIGURE 5. *Siganus vermiculatus* from Celebes, Indonesia (photograph by John E. Randall).

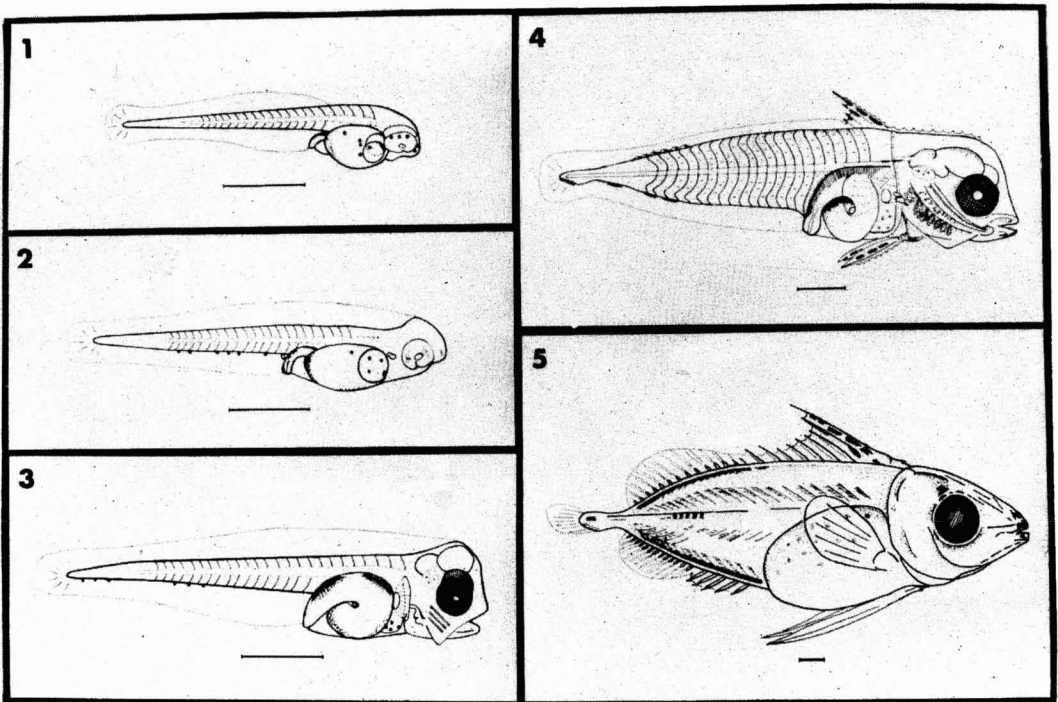


FIGURE 6. Stages in larval development of siganids drawn from larvae of *Siganus canaliculatus* (horizontal line = 0.5 mm): (1) newly hatched larva; (2) 24 hr after hatching; (3) 3 days after hatching; (4) 9 days after hatching; (5) 16 days after hatching.

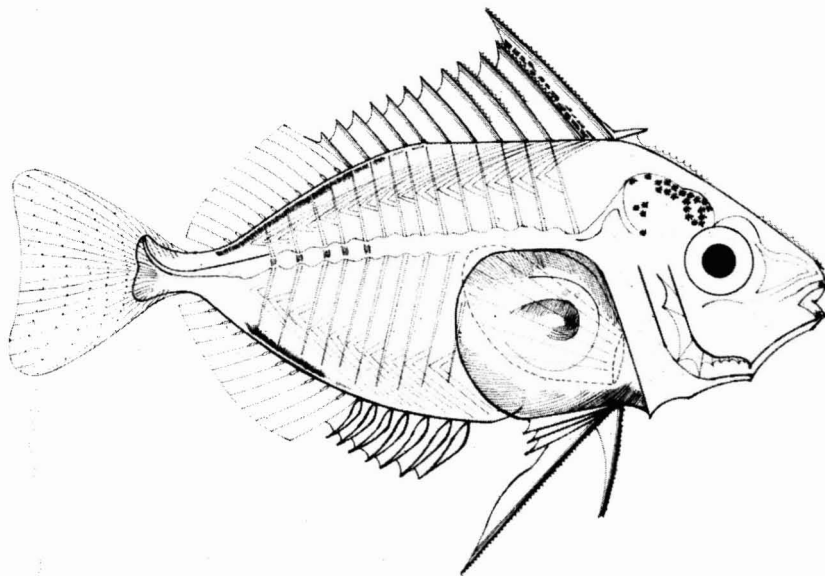


FIGURE 7. Larvae of *Siganus vermiculatus* before metamorphosis (standard length 23 mm).

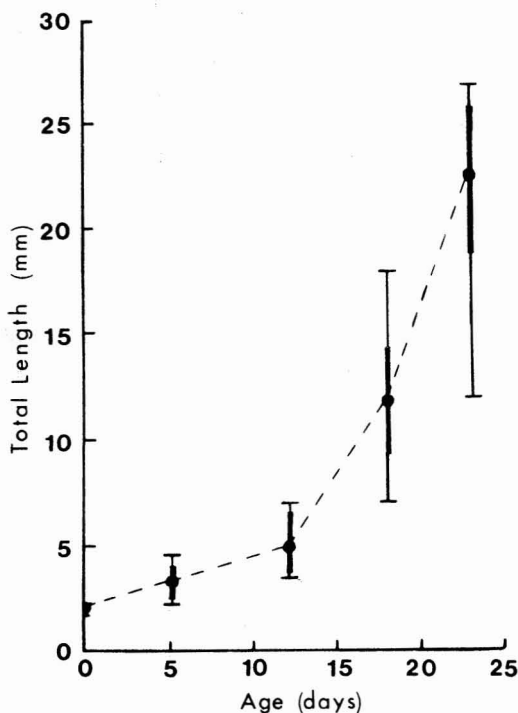


FIGURE 8. Growth curve of larva of *Siganus vermiculatus* ($N = 50$, circles = mean, lines = standard deviation and range).

mangrove roots and other hard substrates. Stomach contents included particles of mangrove bark and various species of algae such as *Enteromorpha* and sea grasses.

Adult fish more than 120 mm long were observed in a variety of habitats, mainly in mangrove swamps and on coral reefs. Observations in mangroves were difficult because of poor visibility and tangled roots. At night, however, beyond the mangroves, the fish could be seen swimming in or out with the tide. Fish were also frequently seen singly or in small groups at coral reefs swimming from one coral head to another, occasionally feeding on algae. On some occasions, schools of several hundred adults were observed. These aggregations occurred in connection with breeding and will be described later. Because the fish were caught or seen simultaneously on the reefs and in the mangroves, it would appear that the fish do not migrate en masse from the reefs with the tides or other factors. Fish caught during the day had full stomachs, indicating that feeding takes place both by day and night. Stomach contents varied with site of catch: in fish on the reef, algae such as *Sargassum* sp. and *Halimeda* sp. were found in the gut; in fish around mangroves, particles

TABLE 1

PERCENTAGE OF FRY COLLECTED FROM ATTRACTORS DURING THE FIRST HALF OF THE LUNAR MONTH THROUGHOUT TWO BREEDING SEASONS

DAY OF LUNAR MONTH	1974			1975					1976
	DEC.	JAN.	FEB.	MAR.	APR.	OCT.	NOV.	DEC.	JAN.
1	0	0	0.4	0.9	0		4.3	3.7	6.5
2	0	0	10.3	5.0	0	2.3	8.1	24.0	23.7
3	23.2	11.8	21.6	8.9	0	29.6	34.5	24.0	29.8
4	40.0	31.5	22.8	25.2	0	37.3	41.8	37.3	23.7
5	18.4	27.6	5.6	14.3	0	11.2	6.0		16.3
6	16.0	18.1	30.2	15.2	0	6.1	4.1	6.6	
7	1.6	2.3	2.6	16.1				3.5	
8	0	0	1.7	3.6		9.3	1.5	0.9	
9	0.8	0	0	3.8		2.0		0	
10	0	2.3	0	3.6		2.1			
11	0	0	0	3.4			0.6		
12		2.3	4.7	0		0			
13	0	3.9	0	0		0			
14		0	0			0			
No. of fry	125	127	232	559	0	983	1,714	2,332	1,225

NOTE: Eighteen attractors were set from December 1974 to April 1975. Sixty-five attractors were set from October 1975 to January 1976.

of mangrove roots and epiphytic algae which grow on mangrove roots were the primary gut constituents.

No observations were recorded of *Siganus vermiculatus* sleeping in the field. The fishes were often seen swimming or actively feeding at night. In aquaria, however, the fish were seen sleeping at night with their bodies pressed against the sides of solid objects. Once illuminated they started to move slowly backward for a few seconds before jerking suddenly away from the light.

The largest fish measured in this study was a female 40 cm long (1800 g) and a male 36 cm long (1200 g), both from Ngau Island (Figure 1). In all samples collected, females were larger than males. In a series of samples collected throughout the year from Raviravi, females of about 29 cm (600 g) and males of 28 cm (500 g) were the most abundant (Figures 10 and 11). Larger fish were caught around Suva. The modal length of adult females was around 31 cm (700 g) and of males 30 cm (600 g).

Monthly gonad examination of *Siganus vermiculatus* indicates that it breeds from September to February in Fiji, corresponding with a rise in water temperature. The gonadal

index reaches its peak between November and February (Figure 12), when the temperature is highest (Figure 13). Females start to reproduce at 1 yr or when slightly younger. The smallest mature female caught was 12 cm (240 g). The smallest adult fish developed ripe ovaries only late in the season. Older females more than 25 cm long (400 g) that have bred in previous years start to reproduce at the beginning of the season (Figure 12).

Siganus vermiculatus spawn during the morning of the 7th or 8th day of the lunar month. The lunar cycle is confirmed by the following observations: (1) spawning in captivity occurred only in the morning of the 7th and 8th days (Table 2); (2) gonads of all mature females were ripe before these days and were spent afterwards (Table 2); (3) peaks in numbers of fry collected at the attractors occurred 3 wk after spawning (Table 1), which corresponds with the time between spawning and metamorphosis of larvae reared in captivity. That all females caught on the reefs or in the mangroves had ripe eggs before the spawning days and were spent thereafter indicates that the same females spawn in successive months throughout the breeding season.

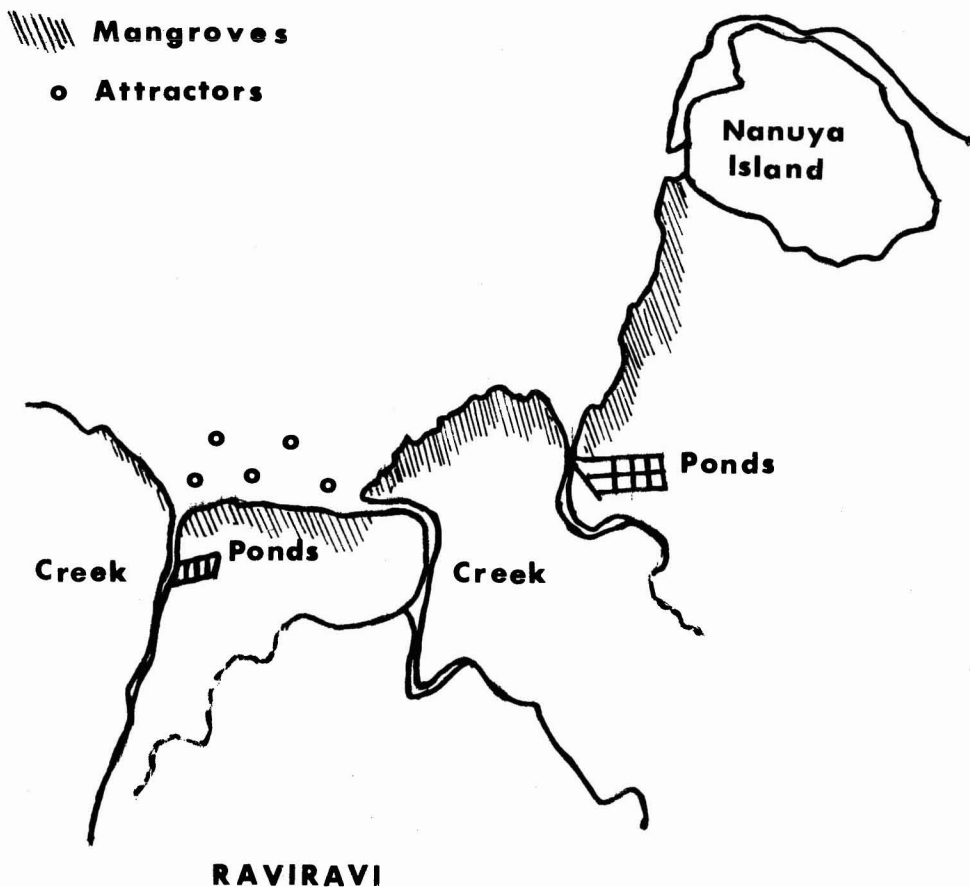


FIGURE 9. Site of study in Raviravi, Fiji Islands, with locations of attractors.

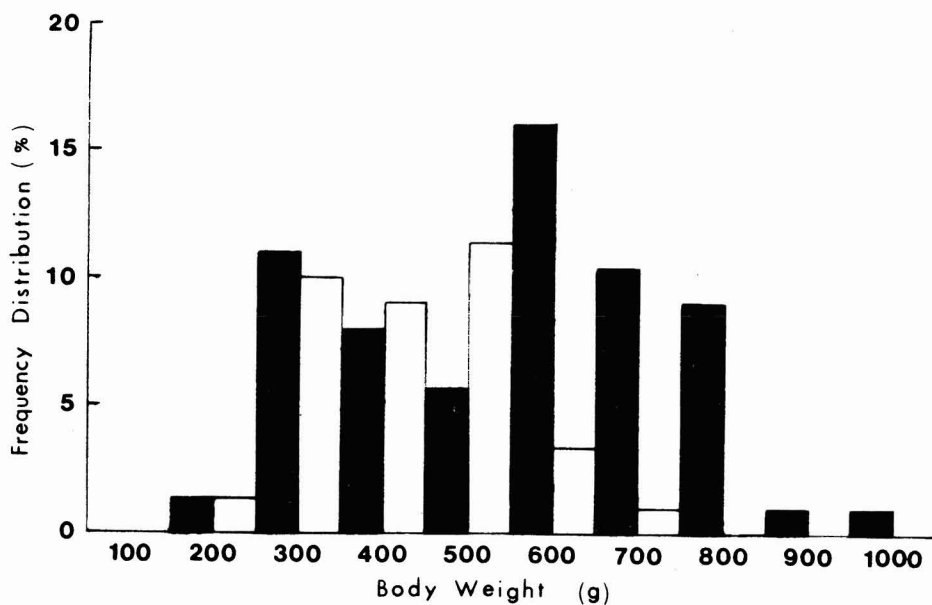


FIGURE 10. Weight-frequency distribution (in percent) of adult fish sampled in Raviravi, Fiji Islands (black = females, white = males, $N = 58$).

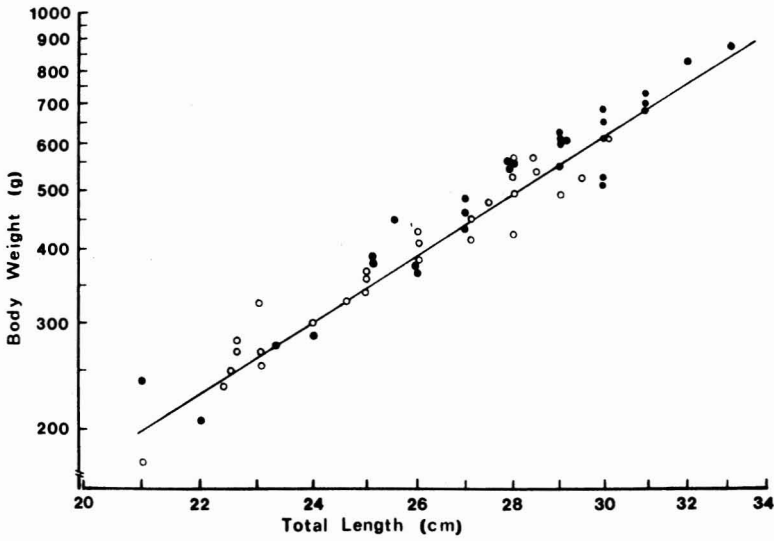


FIGURE 11. Weight-length relationship of all fish within the breeding size, sampled in Raviravi, Fiji Islands (black circles = females, white = males).

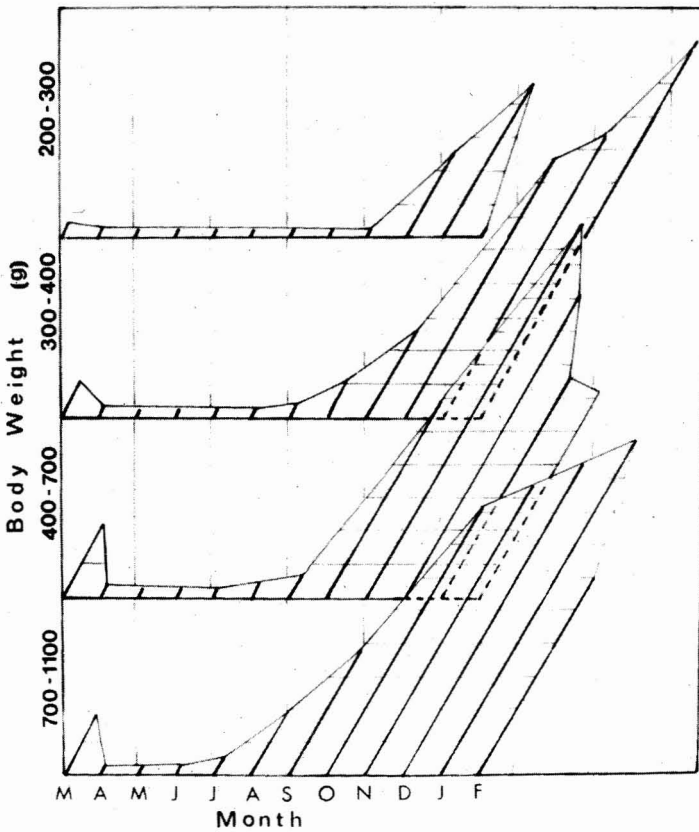


FIGURE 12. Monthly average of gonadal index according to size groups (diagonal units represent 1 percent of body weight).

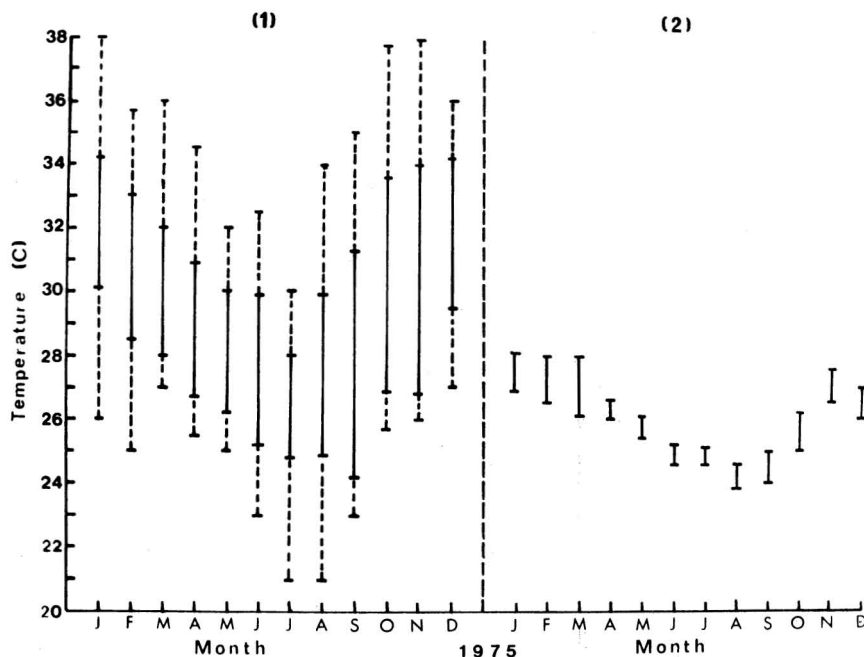


FIGURE 13. Monthly temperature fluctuation in (1) earthen rearing ponds in Raviravi and (2) in the open sea in Fiji waters.

Prespawning and spawning behavior were observed twice in the field and several observations were made of fish in captivity. Spawning behavior was observed only the 7th and 8th days of the lunar month. Prespawning behavior was observed in Suva on the morning of 19 January 1975 over a period of 20 min at 0700 hr. A school of large adults numbering several hundred individuals was swimming actively in circles. The school was concentrated in one location for the duration of the observation. The fish could be approached to a distance of half a meter before they retreated. Murky water prevented more detailed observations, and no fish were collected.

A second spawning observation was made on the mornings of 13 and 14 October 1975, off Ngau Island (Figure 1) at first light (about 0530 hr). The school was located, as had been the school observed in Suva, in a slight depression on a sandy bottom at a depth of 5 to 6 m surrounded by coral heads. The school of more than 200 individuals was aggregated over an area of some 50 m². Within the school, groups of three to eight fish interacted sepa-

ately, one large adult fish swimming in circles with undulating movements followed by smaller individuals. The smaller fish, presumed to be males, occasionally touched the anal region of the large fish, presumed to be female, with their snouts. This behavior, which lasted an hour, took place near the sandy bottom, the females often touching the bottom with their flanks while swimming on their sides. The fish were not disturbed when a diver approached within a distance of half a meter. The entire school did retreat, however, when some individuals were speared, and swam to deeper water only to return within minutes and resume their behavior.

The fish speared the first morning included three large females of 30 to 40 cm (1600 to 1800 g) and two males of 35.5 and 36 cm (1200 and 1300 g, respectively). The females had ripe, opaque oocytes 400 μ m in diameter in the large ovaries (158 to 180 g), and the males had running milt. Two females of 39.5 and 40 cm were caught the following morning. Both had transparent ovulated eggs of more than 600 μ m in the lumen of the ovary. These

TABLE 2

DATES OF EVENTS INDICATING SPAWNING IN RELATION TO LUNAR CYCLE (NUMBERS REPRESENT DATES OF OCCURRENCE OF THE OBSERVED EVENTS)

MONTH	NEW MOON	GRAVID FEMALES FROM NATURE	SPAWNING IN CAPTIVITY	SPENT FEMALES FROM NATURE	PEAKS OF FRY COLLECTION
October 1974	23	22			16
November 1974	23	22			16
December 1974	22	21	22, 24	24	17
January 1975	19	19, 20	22		14
February 1975	18	19			13
March 1975	20				15
October 1975	12	11, 13, 14			9
November 1975	10	9	11, 12		6
December 1975	9	8		14	5
January 1976	10	8		12	3
February 1976	8	6		11	1

observations suggest that the fish were actually spawning on the second day, whereas only prespawning behavior was observed on the first day. No eggs were collected or seen on the site, perhaps because of the small size of the transparent, demersal eggs. The school remained in the spawning area for about 4 hr and was last seen on both days about 0930; no fish were observed at 1000, 1200, 1600, or 1800 hr.

A distinct change in color pattern was noticed during prespawning and spawning behavior. In both males and females the vermiculated pattern nearly disappeared and was replaced by a wide horizontal dark stripe which divided the body into two equal brighter sections. The dorsal, caudal, and anal fins became darker than usual around the edges giving the impression of a black frame around the body. The color pattern associated with spawning behavior was also observed in an aquarium. The fish changed their color pattern within 3 to 5 sec while chasing each other in a manner similar to that described for prespawning behavior described above. The aquarium observations occurred on the morning of 21 January 1975 (the first quarter of the new moon) between 0700 and 0930 hr. No spawning occurred in the aquarium, although the two females had ripe oocytes and the males released milt upon pressure.

Eight spawnings were obtained in captivity.

All occurred the mornings of the 7th or 8th day of the new moon. Spawning behavior was not observed because the water in the concrete spawning tanks was murky, and spawning was determined by the presence of eggs and from biopsies. The number of eggs spawned at one time was estimated at more than 350,000 for a female of 240 g.

Several experiments planned to interfere with the lunar cycle of spawning by hormonal treatment (Popper, May, and Lichatowich 1976) gave negative results. Shading the tanks or exposing them to moonlight had no effect on the cycle either.

Growth Rates

Observations on growth rates in nature and in captivity revealed that *Siganus vermiculatus* is a fast grower compared to other siganid species. Fry stocked in ponds reached reproductive size of 240 g within 9 mo (Figure 14).

Growth rate of the fish in nature, at least during the initial 5 mo, was similar to that observed in ponds. Size groups in catches of fry and juveniles were identified during the second half of February 1974 when fish of the following size groups were netted during night torching: 21–28 mm (101 fish); 35–50 mm (31 fish); 72–90 mm (12 fish). These fish represented age groups of one, two, and three months, respectively. Forty larger fish, in-

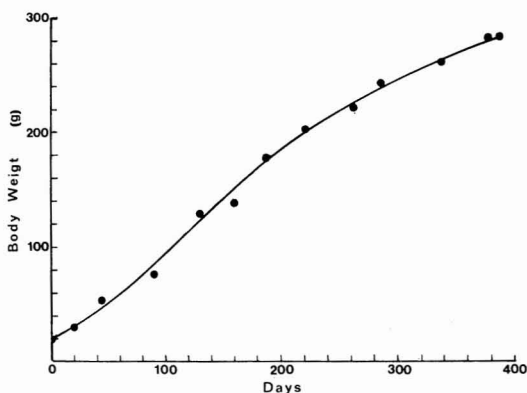


FIGURE 14. Growth rate in weight of *Siganus vermiculatus* in earthen ponds in Raviravi, Fiji Islands.

cluding 12 fish of 12–13 cm (5 mo old), were caught in a net set in front of mangroves. The remaining fish, between 17 and 21 cm, could not be aged according to size and may have been fish of the previous year's spawning.

Tolerance to Physicochemical Parameters

In nature and in ponds fish were found to be tolerant of a wide range of temperature, salinity, and pH (Figures 13, 15).

Fry were caught in water with a salinity of 2 ppt and survived exposure to fresh water for 24 hr. Juveniles of 50 to 70 mm tolerated dissolved oxygen levels as low as 1.2 ppm at a temperature of 32°C without showing signs of distress over 100 min. At 1.1 ppm, however, extremely fast and wide opercular movements were observed, and the fish started erratic jumps to the water surface.

Temperature in the ponds in which the fish were reared often fluctuated between 24 and 32°C in the course of 24 hr. The range of temperatures was between 19 and 38°C. Similar temperatures were recorded in the mangrove swamp. Fish of 200 to 240 g survived a temperature of 38°C for more than 2 hr when water level was lowered on a sunny day. Salinity in the ponds ranged between 10 and 50 ppt and pH levels varied between 6.5 and 10.0 (Figure 15).

The larvae were more sensitive than were the adults to fluctuations in temperature. No

larvae survived in a pond with a range of 24 to 34°C and daily fluctuations of 4 to 6°C (Figure 16). However, they did survive daily fluctuations thereafter. In the rearing tanks salinity ranged from 26 to 34 ppt, and pH levels were between 8 and 10 (Figure 16).

DISCUSSION

Identifying siganids as to species is notoriously difficult because of their morphological uniformity (Woodland and Randall 1979), which includes the length-weight relation (e.g., Figure 3 and Von Westernhagen and Rosenthal 1976).⁴ Siganids are also highly specialized in terms of anatomy and feeding habits (Hiatt and Strasburg 1960). It is surprising, therefore, that siganids occupy a remarkably wide diversity of shallow water habitats (Lam 1974, Popper 1979), including coral reefs (Woodland and Allen 1977, Woodland and Randall 1979), sandy and rocky bottom with or without vegetation (Popper and Gundermann 1975, Hasse, Madraisau, and McVey 1977), lagoons and river mouths (Munro 1967), and mangrove swamps.

The siganid family can be divided into two groups of species on the basis of habitat, behavioral characteristics, and coloration. One group includes species that live in pairs, are site-tenacious, and are brightly colored, for example, *Siganus corallinus* (Valenciennes), *S. puellus* (Schlegel), and *S. (Lo) vulpinus* (Schlegel and Muller). These species are associated strictly with coral reefs (Popper 1979). The other species at some stage of their life are seen in schools that may move over substantial distances, for example, *S. rivulatus*, *S. luridus*, and *S. canaliculatus* (Popper and Gundermann 1975, Hasse, Madraisau, and McVey 1977). These fishes are gray or drab in color, usually matching the color of the substrate.

The coral-dwelling siganids are fragile fish, sensitive to changes in physicochemical para-

⁴ Von Westernhagen and Rosenthal (1976) presented a series of graphs which show almost identical length-weight relations in all six species they collected in the field in the Philippines.

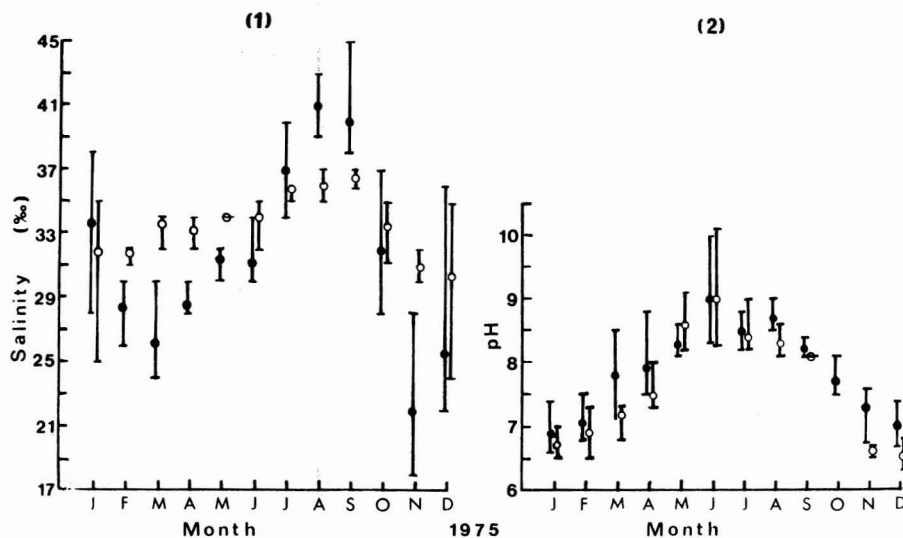


FIGURE 15. Monthly fluctuations in (1) salinity (2) pH in the rearing ponds and mangroves (circles represent mean, line = range, black circles = ponds, white = mangroves).

meters (Popper 1977), whereas members of the second group are hardier and apparently resistant to considerable change in salinity and temperature (Popper 1977). In this latter group, *Siganus vermiculatus* is an extreme example and an exception in some respects. Although it breeds in large schools, this species is most often seen moving solitarily or in small groups. It does not display the interspecific aggressive behavior of coral-dwelling siganids (Popper 1977, 1979). Most other species belonging to the second group form large schools as fry, for example, *S. rivulatus*, *S. luridus* (Popper and Gundermann 1975), and *S. canaliculatus* (Hasse, Madraisau, and McVey 1977). Post-larvae and fry of *S. vermiculatus*, however, are always seen singly or in small groups of up to 10 individuals. They live at least partly in mangrove swamps, a habitat with substantially fluctuating physicochemical parameters (Figures 12, 14), and are accordingly more tolerant of changes in temperature, salinity, and oxygen levels than any other siganid on record, for example, *S. rivulatus*, *S. luridus* (Popper and Gundermann 1975), and *S. argenteus* (Tobias 1976). In terms of coloration, *S. vermiculatus* appears at first glance

to possess a striking color pattern that may stand out against most backgrounds. Considering the play of light and shade in mangrove swamps, however, the vermiculated pattern may have some camouflage value.

Siganus lineatus is also found in mangrove habitats. It is as tolerant of physicochemical fluctuations as is *S. vermiculatus*: fry were found in freshwater creeks in the New Hebrides and New Caledonia, and juveniles of 10 to 20 cm were reared successfully in ponds in a reclaimed mangrove area in New Caledonia where conditions were similar to those in the ponds in Raviravi (Popper, unpubl).

Our findings suggest that *Siganus vermiculatus* and *S. lineatus* rarely overlap in their geographical distribution. During the present study *S. vermiculatus* and *S. lineatus* were never found together on the same island. Numerous observations were made in the field—local markets, fishing boats on the Great Barrier Reef (Heron Island, One Tree Island), and mangrove areas in the New Hebrides, New Caledonia, the Solomon Islands, Palau (Koror and Babelthuap), the Philippines, and the Fiji Islands. We recorded *S. lineatus* at all these localities but found *S. vermiculatus* only

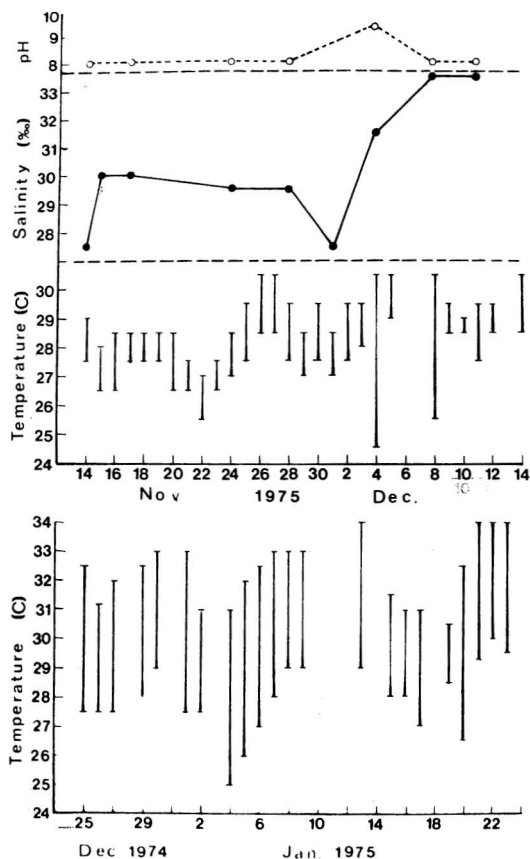


FIGURE 16. Daily changes in physical conditions in ponds used for rearing larvae of *Siganus vermiculatus*: top, minimum and maximum temperatures, salinity, and pH in 80 m³ cement tank; bottom, temperature in an earthen pond in which no larvae survived to metamorphosis.

in the Philippines and Fiji Islands. The record of *S. lineatus* from Manila, Philippine Islands (Jordan and Seale 1907 in Herre and Montalban 1928) has not been confirmed, while Munro's (1967) record of both species from New Guinea may be based on incorrect identifications. Nor have Woodland's (pers. comm. 1980) findings of *S. vermiculatus* in the mangrove marshes of Palau and north Australia been confirmed.

The eggs and larvae of most siganid species that have been described (*Siganus fuscescens*, *S. canaliculatus*, *S. rivulatus*, *S. luridus*, *S. lineatus*, *S. vermiculatus*) (Soh and Lam 1973,

Manacop 1937, Popper, Gordin, and Kissil 1973, Brian and Madraisau 1977) are demersal and sticky and so similar that it is practically impossible to tell them apart. The one obvious exception is the floating egg of *S. argenteus* (Popper, Pitt, and Zohar 1979), which may partly explain the very wide range of geographical distribution in that species (Popper, Pitt, and Zohar 1979, Woodland and Randall 1979) as compared with the limited range of most other siganids. *S. argenteus* is found throughout the entire distribution of the family, extending from the Red Sea in the west⁵ to Tahiti (pers. obs.) and Pitcairn Island (J. E. Randall, pers. comm. 1981) in the east. Other siganid species appear to replace each other within that range.

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⁵Two species, *Siganus rivulatus* and *S. luridus*, have secondarily expanded this range of distribution by penetrating into the Mediterranean via the Suez Canal (Ben-Tuvia 1964).

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